Sexual selection and sympatric speciation

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Ecological versus Sexual Selection models of Sympatric Speciation: a Synthesis

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ABSTRACT

Sympatric speciation is a composite phenomenon requiring both ecological differentiation and the evolution of a mating structure that induces reproductive isolation. Ecological and sexual selection models have addressed these two aspects of sympatric speciation separately. We briefly discuss the recent results of these models and argue that the evolution of ecological and mating strategies are mutually dependent processes rather than independent phenomena corresponding to incompatible views of sympatric speciation. Then, we consider a combined model incorporating ecological interactions and sexual selection. In this model, sympatric speciation is initiated by simultaneous evolutionary branching of ecological strategy, leading to ecological differentiation, and mating strategies, resulting in assortative mating. Both types of evolutionary branching can be understood as the outcome of a competition process in which individuals compete for a spectrum of either ecological resources or mating opportunities. Speciation is completed when a linkage disequilibrium between ecological and mating types splits the population into two ecologically differentiated and reproductively isolated groups. Using a combined analytical and individual-based simulation approach, we illustrate the different dynamical regimes and characterize the necessary conditions for sympatric speciation in the model.

INTRODUCTION

The recent empirical and theoretical interest in sympatric speciation has produced a multitude of theoretical models (e.g., Kawecki, 1997; Payne & Krakauer, 1997; Van Doorn *et al.*, 1998; Dieckmann & Doebeli, 1999; Higashi *et al.*, 1999; Kondrashov & Kondrashov, 1999; Drossel & McKane, 2000). Some of these models are very specific (e.g., Van Batenburg & Gittenberger, 1995), others are more general, but all of them conclude that sympatric speciation is theoretically very well feasible (for recent reviews see Via, 2001, Turelli *et al.*, 2001). This conclusion is in striking contrast to the conclusions based on classical models of sympatric speciation (e.g., Maynard Smith, 1966; Felsenstein, 1981; Rice, 1984), which almost universally discarded sympatric speciation as a plausible mode of speciation (Via, 2001). Yet, superficially at least, the recent models are quite similar to the classical models.

This paradox is resolved by two recent theoretical developments. These developments originate from different lines of research, which address two longstanding difficulties in the theory of sympatric speciation (Kondrashov & Mina, 1986). First, sympatric speciation requires, almost by definition, the evolution of a specific mating structure enabling reproductive isolation. Classical models (Maynard Smith, 1966; Felsenstein, 1981; Rice, 1984) had problems to explain the evolution of assortative mating under general and plausible conditions. More recently (Wu, 1985; Liou & Price, 1994; Van Doorn *et al.*, 1998; Higashi *et al.*, 1999; Takimoto *et al.*, 2000), it has been shown that these problems can be overcome if sexual selection is the driving force behind the evolution of reproductive isolation. Second, reproductive isolation is not sufficient to ensure the sympatric coexistence of daughter species. In view of the ecological principle of competitive exclusion, the species can only survive if reproductive isolation is associated with ecological differentiation. Only recently (Metz *et al.*, 1996; Geritz *et al.*, 1998), evolutionary branching theory has provided a plausible mechanism for the evolution of ecological polymorphism in the presence of disruptive selection.

Based on these new insights, a new generation of 'ecological' and 'sexual selection' models of sympatric speciation has been developed. These approaches will be briefly reviewed below. Unfortunately, an integration of both research lines has not yet been achieved. Ecological speciation models (reviewed by Schluter, 2001) focus on ecological differentiation without much attention for the mechanisms underlying the evolution of mating structure. Sexual selection models (reviewed by Panhuis *et al.*, 2001) focus on the process leading to reproductive isolation, usually neglecting ecological divergence. We will argue that both approaches present mutually dependent rather than conflicting explanations of sympatric speciation. To provide a conceptual bridge between them, we will present and analyze a model that integrates the ecological and sexual selection aspects of sympatric speciation. Our main objectives are to investigate the origin of ecological polymorphism and

the evolution of mating strategies within the same formal model, in order to characterize the conditions under which sympatric speciation occurs, to investigate the mutual dependence of ecological differentiation and the evolution of assortative mating, and to identify the common mechanism underlying these two aspects of sympatric speciation.

THE EVOLUTION OF POLYMORPHISM IN THE PRESENCE OF DISRUPTIVE SELECTION

The starting point of ecological models is that sympatric speciation results from disruptive selection. However, disruptive selection alone is not sufficient for speciation to occur. Consider, for example, a species that has access to a range of alternative habitats (e.g., from wet to dry) and assume that, due to external factors, individual fitness is highest in the extreme habitat types and lower in intermediate habitat types. Accordingly, selection is disruptive and one might expect that the population will split into two ecotypes, one specialized on living under wet conditions, and the other specialized on living under dry conditions. In contrast to this expectation, however, such a population will become monomorphic for one of the specialist strategies. In fact, the population will only experience disruptive selection if it starts exactly at the fitness minimum. If the initial state is slightly shifted towards one of the extremes, the population will experience directional selection enhancing the initial bias.

Hence, at first sight at least, populations tend to evolve away from fitness minima where selection is disruptive. This fundamental problem has only recently been resolved (Abrams *et al.*, 1993; Metz *et al.*, 1996), at least for asexual populations. The resolution is based on the insight that selection is usually not externally imposed, as in our example, but frequency dependent. Moreover, selection pressures may vary in strength and direction in the course of evolution, as a result of a feedback between evolutionary and ecological processes. Under such circumstances, evolution may drive the population towards a point where it experiences disruptive selection (Abrams *et al.*, 1993), which subsequently induces polymorphism (Metz *et al.*, 1996). This phenomenon is named 'evolutionary branching'.

To explain this further, we will now consider the example of resource competition as a general ecological interaction that can give rise to evolutionary branching (FIGURE 1). In line with recent models (e.g., Metz *et al.* 1996; Doebeli & Dieckmann, 2000), let us assume that individuals compete for a continuum of ecological resources, distributed according to some fixed resource distribution function (shown in gray in FIGURE 1). Individuals compete for resources locally in resource space, that is to say, individuals do not consume all resources but rather they are specialized to some extent on particular resources. This is reflected by an individual's resource utilization function, the location of which is determined by a quantitative, heritable trait that we will refer to as the individual's ecotype. As competition affects fitness, ecotype is under natural selection, the direction and intensity of

which depends on the resource distribution and on the frequency and resource utilization characteristics of the set of ecotypes present in the population.

Consider a population that is monomorphic for a certain ecotype that does not match the ecological optimum of maximal resource availability (FIGURE 1A). Such a population is not evolutionarily stable: a mutant that is closer to the ecological optimum will be favored by selection because it utilizes resources that are more abundant. Eventually, such a mutant will outcompete the resident ecotype, and in a series of such mutation/substitution events, evolution will drive the population towards the peak of the resource distribution.

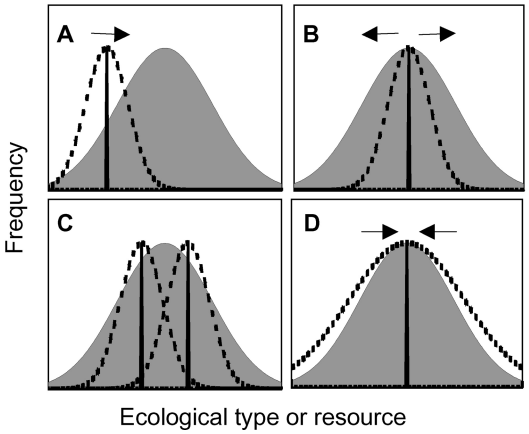


FIGURE 1 – EVOLUTIONARY BRANCHING IN COMPETITION MODELS

Individuals compete for resources that are distributed according to a fixed resource distribution function (shown in gray). An individual's ecotype corresponds to the location of its resource utilization curve (dashed line), which delimits the spectrum of resources that can be utilized. (A) A population that is monomorphic for ecotype (solid line) will evolve towards the peak of the resource distribution. (B) In the case of an ecological specialist, i.e. if the width of the resource distribution is larger than the width of the resource utilization curve, the population experiences disruptive selection once located at the peak of the resource distribution. (C) This leads to evolutionary branching, after which the population becomes dimorphic for ecological type. (D) In the case of an ecological generalist, the population will evolve towards the peak of the resource distribution and remain there.

Once there, however, the population experiences disruptive selection (FIGURE 1B): because of the specialist resource utilization strategy of the population, the resources in the tails of the resource distribution are hardly competed for. Mutants that utilize the tails of the resource distribution gain a competitive advantage, which more than outweighs the lesser availability of those resources. Such mutants can invade the population, which is therefore evolutionarily unstable, and, in this sense, located at a fitness minimum.

The population can only escape from this fitness minimum if it undergoes evolutionary branching and becomes dimorphic for ecotype (FIGURE 1C), since any monomorphic population would be driven back to the ecological optimum again. Evolution eventually leads to a stable situation where selection for avoidance of competition with the other ecotype balances selection towards the ecological optimum.

The mechanism sketched above works only for ecological specialists, with a narrow utilization curve relative to the distribution of available resources. For an

ecological generalist (FIGURE 1D) the competitive advantage of utilizing resources in the tails of the resource distribution will be much smaller than in the specialist case, since the generalist still competes for those resources rather efficiently. Therefore, a mutant that utilizes resources not at the ecological optimum will suffer more from the disadvantage of the lesser availability of those resources than it benefits from its competitive advantage, and selection will therefore be stabilizing towards the ecological optimum. Consequently no mutants can replace the resident ecotype at the ecological optimum, and in this sense, the monomorphic resident population is evolutionarily stable.

The intuition behind the occurrence of evolutionary branching of ecological strategies in resource competition was confirmed, at least for asexual populations, by a mathematical formulation based on Lotka-Volterra type population dynamics (Metz *et al.*, 1996). In fact, evolutionary branching has been shown to occur in a variety of mathematical models of asexual populations in different ecological settings, and can therefore be considered a general explanation for the evolution of polymorphism in the presence of disruptive selection (Doebeli & Ruxton, 1997; Geritz *et al.*, 1999; Kisdi, 1999).

THE PROBLEM OF RECOMBINATION

A solution of the problem of the origin of polymorphism under disruptive selection does not solve the whole problem of sympatric speciation. In sexual populations, a second problem arises. As soon as a polymorphism originates in a sexual population, it will immediately be destroyed when mating is random. This is because mating between different ecotypes will yield intermediary and less fit hybrids, and the random recombination of genotypes will reshuffle co-adapted gene complexes. In order to overcome these problems, assortative mating is required.

However, it is not self-evident that assortative mating will evolve and whether the specific association between ecological and mating type loci will develop. These issues were addressed in several classical models of sympatric speciation (Felsenstein, 1981; Rice, 1984). These models have shown that the required association between ecological type and mating type can, in principle, evolve, but only under conditions of strong linkage or pleiotropy between ecological and mating loci, such that, essentially, ecological and mating characters are determined by a single locus or trait. Such a scenario may apply to certain biological systems, but in general weaker pleiotropic interactions are to be expected (Felsenstein, 1981). For weak pleiotropic interactions between ecological and mating loci it requires unrealistically strong disruptive selection to overcome the randomizing effects of recombination.

Dieckmann & Doebeli (1999) argue that these problems can partially be overcome by a stochastic, individual based description of the process. In their model, assortative mating did evolve in a finite population located at a branching point, leading to both divergence of ecotypes and reproductive isolation. This occurred

for competitive and various other types of ecological interactions (Doebeli & Dieckmann, 2000). Hence, it is possible, at least in principle, that a sexual population undergoes evolutionary branching. However, selection for assortative mating is weak in Dieckmann & Doebeli's models, and only acting at the branching point. This is because only a phenomenological description of mating behavior is given and the mechanism underlying assortative mating is not specified. It is more plausible that assortative mating is the outcome of the evolution of male and female mating strategies. This issue is being addressed in the recent sexual selection models of sympatric speciation.

SEXUAL SELECTION AND THE EVOLUTION OF ASSORTATIVE MATING

Sexual selection models, which explicitly take into account the interaction of male and female mating strategies, typically assume different male and female sex roles: female reproductive success is largely determined by the quality of the offspring produced, whereas male reproductive success is limited by the number of females that can be fertilized. Because of these asymmetries, there will be strong competition for fertilizations among the males and females will exert mate choice if this enables them to mate with a higher quality male (Andersson, 1994).

In the context of speciation, models have focused on the evolution of female preferences for male ornaments by runaway sexual selection. This mechanism, originally proposed by Fisher (1930) as a verbal argument, and later confirmed by theoretical models (O'Donald, 1980; Lande, 1981; Kirkpatrick, 1982), proposes that male traits and female preferences for those traits will become genetically correlated because of non-random mate choice. Once this correlation is established, female preference for more extreme male traits will result in more extreme female preferences, because of a correlated selection response. Because of this positive feedback, preference and trait coevolve in a rapid runaway process, until halted by counteracting natural selection pressures.

Runaway sexual selection is interesting for speciation for two reasons. First, the evolution of preferences for male ornaments provides a mechanism of strong pre-zygotic reproductive isolation. Second, and in contrast with good genes models, the direction of the runaway process is arbitrary. This could result in rapid evolution of reproductive isolation between allopatric populations (Lande, 1981). For sympatric speciation however, there would have to be simultaneous runaway processes in different directions within a single population. In a previous model, specifically addressing speciation of cichlid species (Van Doorn *et al.*, 1998), we showed that simultaneous runaway processes within a single population are attainable. Moreover, Higashi *et al.* (1999) and Takimoto *et al.* (2000) provided an important proof of principle that sexual selection alone is sufficient to split a population into two reproductively isolated groups.

There are however a number of problems. First, it is not clear how the reproductively isolated daughter species can coexist in the absence of ecological differentiation. Second, there is the fundamental problem that disruptive sexual selection has similar properties as disruptive natural selection, and it is a similarly delicate affair to maintain a long-term polymorphism in the presence of disruptive sexual selection as it is for disruptive natural selection. In the models, this translates for instance into neutral stability of relevant equilibria and requirements of symmetric parameter conditions, large initial genetic variance of female preference and male trait or very strong selection.

EVOLUTIONARY BRANCHING OF MATING STRATEGIES

The problem of maintaining polymorphism in the presence of disruptive selection is similar for both natural and sexual selection. This similarity leads one to wonder whether processes analogous to the evolutionary branching in the ecological models could also occur as a consequence of sexual selection, resulting in the evolutionary branching of mating strategies. In fact, in another paper (CHAPTER 2 of this thesis) we analyzed a model in which such mating type branching does indeed occur, resulting in a stable polymorphism of mating strategies.

In order to explain this further, let us now consider a verbal model in which male and female mating strategies are determined by heritable mating types. Let us also assume the typical sex roles: all males compete to fertilize a female, and a female chooses a male (actively or passively) based on the compatibility of male and female mating strategies, according to some mate choice or fertilization efficiency function. The model is very general and reflects a variety of specific examples ranging from female preference (female mating type) for male ornaments (male mating type) in lekking birds to the interaction between gamete recognition proteins in marine broadcast spawners (Vacquier, 1998), where sperm proteins (male mating type) interact with egg surface proteins (female mating type) during fertilization.

Under these assumptions, selection on males will be much stronger than selection on females. In FIGURE 2A we consider an extreme case, in which there is a variety of female mating types present in the population (gray distribution), and, because of stronger selection, just a single male mating type (solid black). The spectrum of female mating types that can be efficiently fertilized by the male mating type is indicated by the dashed line, representing the fertilization efficiency function. If we assume that fertilization efficiency is highest when male and female mating types match, then selection on male mating type will drive it towards the maximum of the female mating type distribution. In addition, the distribution of female mating types is not fixed, and evolution will act on it towards optimal matching with male mating type, although the selection pressure on female mating type will be much weaker than on male mating type. When male and female mating type are matched, selection will be stabilizing as long as the distribution of fe-

male mating types is narrow, as in FIGURE 2B. In that case, males can fertilize the full distribution of female mating types with reasonable efficiency. Hence, the competitive advantage of specializing on extreme female mating types does not outweigh the disadvantage of the lesser abundance of those female mating types.

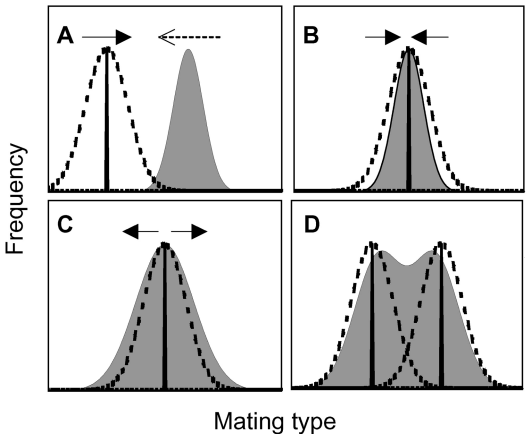


FIGURE 2 – EVOLUTIONARY BRANCHING OF MATING STRATEGIES

In (A), we consider a population that is monomorphic for male mating type (solid black line). Males compete to fertilize a spectrum of female mating types (shown in gray). Fertilization efficiency is highest when male and female mating type match, as reflected by the fertilization efficiency function (shown as a dashed line). This results in strong selection on male mating type, and similar, but much weaker, selection on the female mating type distribution, towards optimal matching of male and female mating types. (B) If the variation of female mating types is small, there is a single optimal male mating type and the population will experience stabilizing selection. (C) When the variation of female mating types becomes larger, however, it pays to specialize on females that are not that efficiently fertilized by the resident male mating type. Then selection becomes disruptive, and the population undergoes evolutionary branching (D), inducing further widening of the female mating type distribution, and the subsequent evolution of assortative mating.

However, when selection of female mating type is sufficiently weak, the distribution of female mating types may widen by mutation pressure, beyond a point where selection on male mating types becomes disruptive (FIGURE 2C). Then, mutant males that specialize on the extreme female mating types can invade, since these are hardly competed for by the resident males, and the population will undergo evolutionary branching of male mating types.

After evolutionary branching, the distribution of female mating types slowly adapts to the dimorphic distribution of male mating types, widening further, which allows male mating types to separate even more, thus lowering competition for fertilizations (FIGURE 2D). In the end, assortative mating can evolve, as a result of linkage disequilibrium between male and female mating type genes.

Note that there is a biological analogy between competition for ecological resources and competition for fertilizations (as also reflected by the analogous choice of notation in FIGURES 1 & 2), which –in the verbal models at least- extends to analogous evolutionary dynamics for ecotype and male mating type.

A SYNTHESIS OF ECOLOGICAL AND SEXUAL SELECTION MODELS

In order to understand sympatric speciation, we will eventually have to analyze the interplay between ecological and mating type branching. As argued above, ecological branching requires assortative mating, the evolution of which might be explained by sexual selection. On the other hand, sexual selection models require ecological differentiation for the coexistence of incipient species. Therefore, it is very likely that in real world systems, both sexual selection and ecological processes will play a role in sympatric speciation (Galis & Metz, 1998). Based on these arguments, we will now proceed by writing a formal model of sympatric speciation. The model will incorporate a minimal description of mating behavior and ecological interactions, which will allow us to further analyze evolutionary branching of mating strategies and ecological branching within the same framework.

GENERAL MODEL STRUCTURE

We consider the evolutionary dynamics of three continuous, heritable, phenotypic traits: ecotype (denoted x), female mating type (denoted p) and male mating type (denoted q). Let us focus on an arbitrary female i. When the female is ready to mate, all males compete to fertilize her. The probability that a particular male j succeeds to fertilize the female is proportional to the male's 'attractivity' for female i, denoted a_{ij}. We keep the model as general as possible and make no assumptions regarding the mechanism of female choice: attractivity and mate choice may be based on any active or passive process (behavioral, morphological or other) that affects the probability that a female mates with a particular male. We assume that attractivity is highest when male and female mating types match. Moreover, we allow for the possibility that attractivity might also be higher when i and j are of similar ecotype, for instance, when individuals occupying similar ecological niches are more likely to meet one-another. Therefore, we take

$$a_{ij} = g_m\left(p_i - q_j\right) g_e\left(x_i - x_j\right), \qquad [1]$$

where here and henceforth g_a denotes a Gaussian function with mean zero and standard deviation σ_a. In particular, the standard deviations of the Gaussian distributions used here, σ_m and σ_e, determine the specificity of mate choice with respect to mating type and ecotype differences respectively (for an overview of the parameters used in the model, consult TABLE 1). In the limit of large σ_e, mating probabilities are independent of ecological differences and determined solely by male and female mating types. Alternatively, in the limit of large σ_m, mating is assortative with respect to ecotype without any dependency on male and female mating types.

When the female cannot find an attractive male, she does not mate. This occurs with a probability that increases with η. This parameter determines the strength of direct selection on female mating preference. When $\eta = 0$, females will

always mate, regardless of their mating preference, and hence there is no direct selection on female mating type p. In contrast, when $\eta > 0$, for instance when searching for mates is costly, or when sperm is limiting, selection will act to match female with male mating type.

Under these assumptions, the probability that female i mates with male j, denoted as α_{ij} is given by

$$\alpha_{ij} = \frac{a_{ij}}{\eta + \sum_{\text{males } k} a_{ik}}. \qquad [2]$$

A fertilized female produces b offspring. Offspring mortality until reproductive age is determined by the intensity of ecological resource competition. Individuals compete for a continuum of ecological resources distributed according to a fixed Gaussian function $g_K(x)$. The intensity of resource competition between two individuals *i* and *j* is taken to decline as a Gaussian function $g_c(x_i - x_j)$ of the difference between their ecotypes. This reflects the assumption that individuals with dissimilar resource utilization strategies compete less intensely. More precisely, competition induced mortality, m_i, is taken to be directly proportional to the intensity of competition with all other individuals and inversely proportional to resource availability

$$m_i = \gamma \frac{\sum_k g_c(x_i - x_k)}{g_K(x_i)}, \qquad [3]$$

where the parameter γ scales the carrying capacity of the system. As argued before (see FIGURE 1), the width of the resource utilization function, σ_c, relative to the width of the resource distribution, σ_K, determines the competitive regime.

We also include direct viability selection on male mating type as an extra source of mortality for males. We normalize male mating type in such a way that $q = 0$ is the optimal mating type for survival, and multiply the survival rate, $1 - m_i$, by an extra Gaussian factor, $g_s(q)$, for males. Adult males and females die at a constant rate. We assume that females reproduce only once during their lifetime. Males may reproduce several times, by fertilizing multiple females.

We will analyze the model by combining two approaches: individual based computer simulations and mathematical analysis. Using the computer simulations, we will illustrate the different types of dynamical behavior of the model. Subsequently, we will try to gain more insight in the processes underlying sympatric speciation by studying a special case of the model using adaptive dynamics methods. In this analysis, we will derive predictions for the parameter conditions under which sympatric speciation occurs. Finally, we will test the robustness of these predictions in the simulation model again, which will enable us to study the effects of stochasticity and more complicated genetics on the model outcome.

TABLE 1 – IMPORTANT MODEL PARAMETERS AND THEIR BIOLOGICAL INTERPRETATION

parameter	biological interpretation
b	birth rate
ε, η	cost of mate choice ($\varepsilon = \eta/\text{number of males}$)
σ_K	width of the ecological resource distribution
σ_c	width of the resource utilization function
σ_e	specificity of mate choice with respect to ecological type
σ_m	specificity of mate choice with respect to mating type
σ_n	width of the female mating type distribution
σ_s	strength of viability selection on male mating type.
σ_v	width of the distribution of mutation sizes
μ	population average female mating type

SIMULATION RESULTS

Simulations were run with overlapping generations, with the following additional assumptions: x, p and q are fully heritable traits that are each determined by a diploid locus. All genes are unlinked and alleles interact additively. Offspring genotypes are determined according to normal Mendelian genetics. We assume a continuum of alleles, that is, the phenotypic effect of each allele is a continuous quantity. Mutation is modeled by altering the phenotypic effect of each allele every generation and independently by a number drawn from a normal distribution with a narrow width σ_v.

We ran simulations for parameter combinations that either precluded or allowed for evolutionary branching. Based on our verbal arguments, we may expect branching of ecotypes (FIGURE 1) to occur in a specialist resource utilization scenario. Quantitatively, as was shown in Doebeli & Dieckmann (2000), this means that the width of the resource utilization function should not exceed the width of the resource distribution, that is, $\sigma_c < \sigma_K$. Moreover, the specificity of mate choice with respect to ecotype, σ_e, may also affect the conditions for ecological branching. We chose to vary the width of the ecological resource distribution, σ_K, in order to simulate a specialist and a generalist resource utilization scenario. Similarly, conditions for mating type branching (FIGURE 2) are likely to be affected by the width of the female mating type distribution relative to the width of the fertilization efficiency function, σ_m. This balance is affected by the width of the mutation distribution, σ_v, the cost of female mate choice, η, and, of course, σ_m. The latter parameter was varied in order to simulate high and low specificity of mate choice.

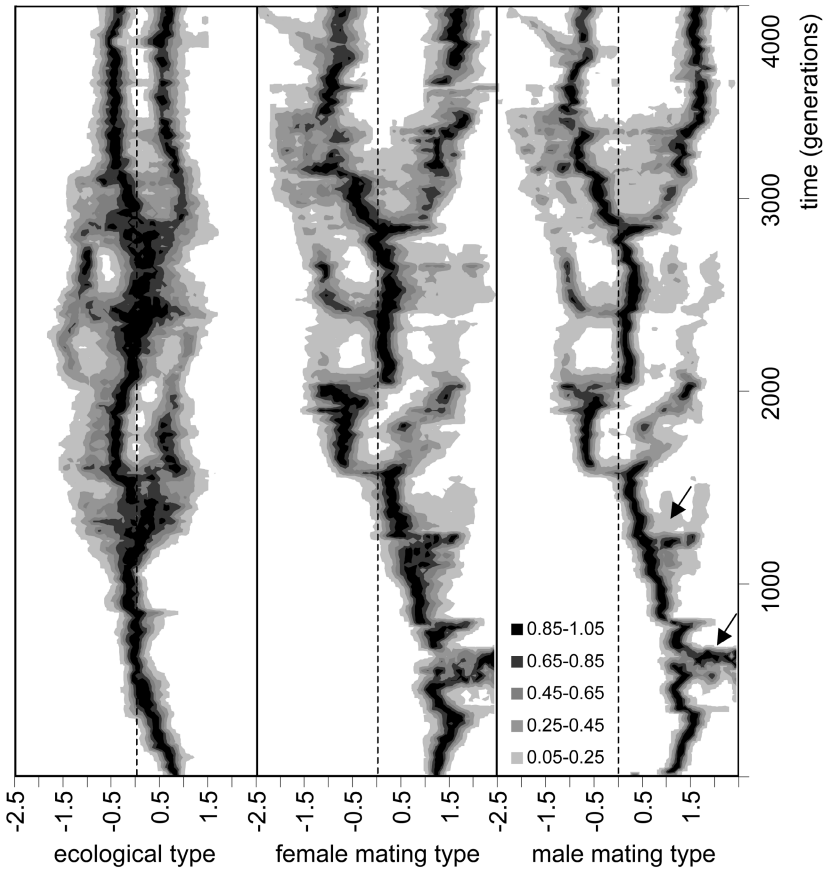


FIGURE 3 – SCENARIO 1: SPECIATION

The three panels show the distribution of ecological and mating types (gray-scale) during 4000 generations of evolution. In the first phase of evolution, ecotype evolves towards the ecological optimum (dashed line). There, the population experiences disruptive selection (the variation of ecological types increases), but cannot undergo evolutionary branching, because assortative mating has not yet evolved. During this initial stage, (<1500 generations) male and female mating type evolve jointly towards the optimum for male survival (dashed line). Several times, polymorphisms of mating types originate (arrows), but these are unstable due to competitive exclusion and viability selection against extreme male mating types. After 1500 generations, simultaneous branching of ecotype and mating strategies repeatedly splits the population into groups that are ecologically differentiated and, at the same time, reproductively isolated. Such branching events may therefore be interpreted as sympatric speciation events. Parameters were $\sigma_c = 0.4$, $\sigma_K = 1.2$, $\sigma_e = 0.6$, $\sigma_m = 0.2$, $\sigma_v = 0.02$, $\sigma_s = 1.0$ $\eta = 1.0$, $b = 4.0$. Furthermore, parameter $\gamma = 5 \cdot 10^{-4}$ kept the population sizes in the simulations close to about 1000 individuals per species.

Sympatric speciation occurs only under conditions that allow for evolutionary branching of both ecotype and male and female mating type (FIGURE 3). In that case, the population splits into distinct clusters, where each cluster can be interpreted as a species, since it is characterized by a unique combination of ecotypes and mating types. Within a species, male and female mating type match with one another, while there are large differences in mating types between species. Because of these mating type differences, species are reproductively isolated from each other. Male and female mating types are highly correlated with each other across the population, as a result of the evolutionary dynamics. This effectively results in assortative mating to a degree high enough to allow for the evolutionary branching of ecotypes and the simultaneous build up of a linkage disequilibrium between the ecological and mating loci. The same processes occur in multilocus simulations (data not shown) where ecological and mating types are coded by multiple loci. In that case, assortative mating is strong enough to overcome the randomizing effects of recombination between ecological loci, which allows for evolutionary branching of ecotypes and speciation.

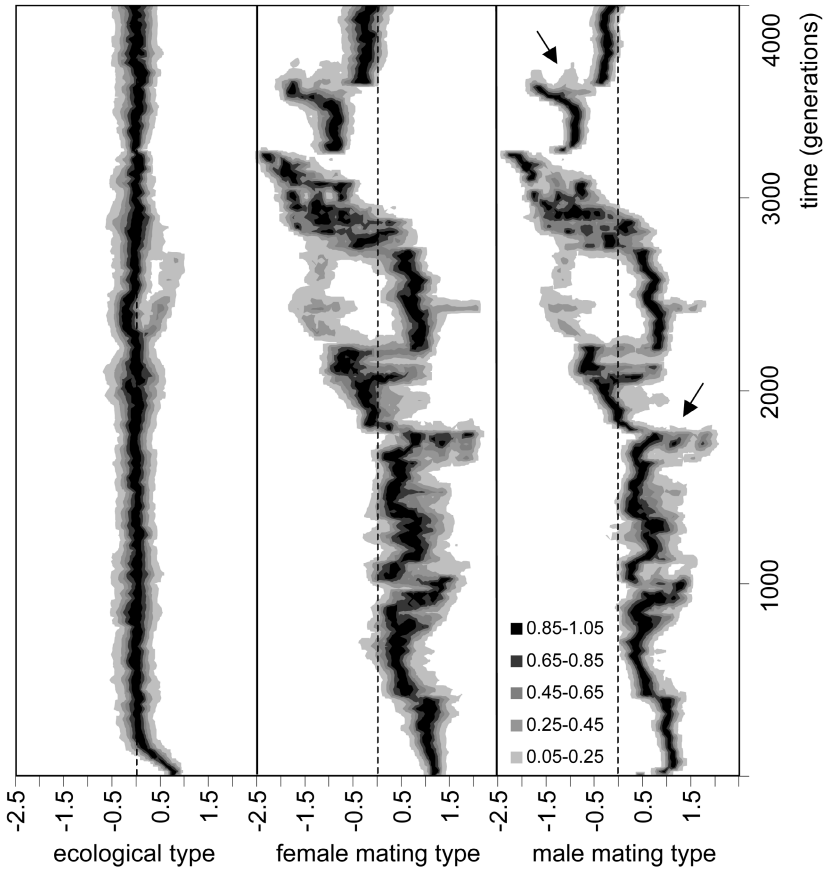


FIGURE 4 – SCENARIO 2: COMPETITIVE EXCLUSION

In this simulation, parameters are as in FIGURE 3, except that $\sigma_K = 0.6$. Now, individuals are ecological generalists and branching of ecological type does not occur. Because of this, polymorphisms in mating types (arrows) cannot persist, due to competitive exclusion.

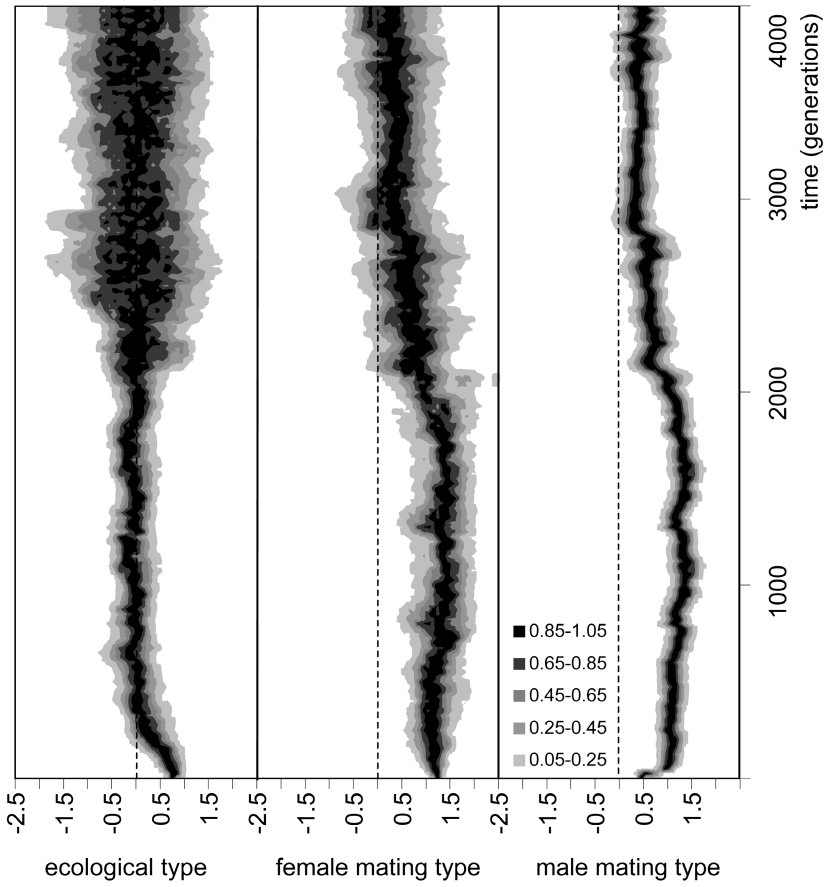


FIGURE 5 – SCENARIO 3: RANDOM MATING

When male and female mating types do not undergo evolutionary branching, as in this simulation, branching of ecological type is excluded. This is because mating is random without polymorphisms of mating types, and random recombination of ecological type genes prevents evolutionary branching. Note that selection on ecological types is still disruptive after convergence to the point of highest resource abundance, as evidenced by the large variance of ecological types. Parameters are as in FIGURE 3, except that $\sigma_m = 0.4$.

Under conditions that preclude the occurrence of ecological branching, the different mating types cannot stably coexist, because competition for ecological resources will drive all but one of the mating types to extinction (FIGURE 4). Alternatively, if there is no polymorphism of mating types, individuals mate randomly. In that case, the evolution of distinct, reproductively isolated ecotypes is prevented (FIGURE 5). Nevertheless, random mating does not preclude the evolution of ecological polymorphism, as evidenced by the broadening of the distribution of ecological types after the ecological optimum has been reached (FIGURE 5). This observation is in line with other models (Kisdi & Geritz, 1999), which suggest for our single locus simulation that disruptive selection at the ecological optimum should result in the evolution of distinct allele types and a stable polymorphism of genotypes. Note that, in our simulations, we do not observe a polymorphism of discrete

types (as in Kisdi & Geritz, 1999), but a broad continuous distribution of ecotypes. This is explained by the smearing that occurs as a result of a rather strong mutation pressure. In multilocus simulations a similarly broad distribution is observed, even under weak mutation pressure, due to recombination.

In order to get more insight in the process of speciation, we need to study the underlying processes of evolutionary branching of ecotype and mating types in more detail. In the next section, we will attempt to find the conditions that are required for both types of evolutionary branching by considering a special case of the simulation model, which will allow us to use the methods of adaptive dynamics.

ADAPTIVE DYNAMICS APPROXIMATION

In our simulations, the variation of female mating types is typically larger than the variation of male mating types (FIGURES 3–5). This can be understood by realizing that the selection pressures on male and female mating types are qualitatively different. For males, the number of females fertilized is the main determinant of fitness, and therefore there is strong competition for fertilizations. Selection is strongly frequency dependent, since a male's reproductive success depends not on his own mating type per se, but rather on its performance in competition relative to the other male mating types present. For females, reproductive success is independent of the strategies of other females and depends solely on the compatibility between female mating type and the male mating types present. If, as we assumed, females are not severely limited by the availability of suitable males (i.e. η is small), then selection pressures on female mating type will be weak. Consequently, the distribution of female mating types will be wider than the distribution of male mating types.

As an approximation of this situation, we will now consider a model in which female mating types vary according to some continuous distribution and where male mating type and ecological type are monomorphic. In order to keep the analysis of the model tractable, we furthermore restrict ourselves to a special case of the simulation model, where traits x, p and q are coded by a single-locus haploid genotype. As in the simulation model, individuals reproduce sexually, allowing for recombination between genotypes. We assume that population size is sufficiently large to allow for a deterministic description of the evolutionary dynamics. Later, we will show that important qualitative as well as some quantitative results derived for this special case apply in general.

INVASION-PROOFNESS AND ATTAINABILITY

We apply standard adaptive dynamics theory (Metz *et al.,* 1996; Geritz *et al.,* 1998) and consider the dynamics of a rare mutant, which differs in either male mating type or ecological type from the resident population. The question is under what conditions this mutant can invade the resident population. The answer to this

question will depend on the mutant phenotype (denoted as y), but also on the resident phenotype (denoted $\hat{y}$), reflecting the effect that the resident has on the biotic and abiotic environment in which the mutant invades. Formally, the invasion prospects of a rare mutant depend on the mutant's long term per capita growth rate $\lambda(y,\hat{y})$, also referred to as invasion fitness (Metz *et al.*, 1996; Geritz *et al.*, 1998). If $\lambda(y,\hat{y}) > \lambda(\hat{y},\hat{y})$, the mutant can invade and a new population dynamical equilibrium will be established, where, usually but not always, the resident is replaced by the mutant. Otherwise, the resident population is proof against invasion by y. If we assume that mutations occur only rarely and in small, discrete steps, this will result, on a longer timescale, in an evolutionary dynamics that consists of a series of such invasion events each followed by the establishment of a new population dynamical equilibrium.

In the case that mutants are only slightly phenotypically different from the resident, the evolutionary dynamics can be derived from the local behavior of the invasion fitness function. In order to do so, we compute the selection gradient

$$\lambda_y(\hat{y}) = \left.\frac{\partial\lambda(y,\hat{y})}{\partial y}\right|_{y=\hat{y}}, \qquad [4]$$

which can be interpreted as follows: if the selection gradient is positive (negative), mutant types that have a higher (lower) phenotypic value than the resident will have a higher fitness, and therefore a selective advantage with respect to the resident. Such a mutant can invade the population and replace the resident. This process is repeated when new mutants arise, and, in a series of mutation/substitution events, evolution will proceed in the direction of the selection gradient.

Interesting resident strategies are those strategies for which directional selection is absent, i.e. strategies for which the selection gradient is zero. Such strategies are referred to as evolutionarily singular strategies (Metz *et al.*, 1996). In generic cases, an evolutionarily singular strategy either cannot be invaded by any mutant strategy, or, alternatively, it can be invaded by all mutants. In the former case, all mutant strategies will have a lower fitness than the evolutionarily singular strategy, which can therefore be characterized mathematically as a fitness maximum with respect to the mutant strategy. In other words, an evolutionarily singular strategy y^* is invasion-proof, when

$$\left.\frac{\partial^2\lambda(y,\hat{y})}{\partial y^2}\right|_{y=\hat{y}=y^*} < 0. \qquad [5]$$

In the latter case, when the evolutionarily singular strategy can be invaded by all mutants, y^* corresponds to a fitness minimum with respect to the mutant strategy and the sign in [5] is reversed.

In the literature, an invasion-proof strategy is often called an evolutionarily stable strategy (ESS; Maynard Smith & Price, 1973). However, an ESS is not necessarily stable in the dynamical sense (Eshel, 1983; Metz *et al.*, 1996; Taylor, 1996; Weissing, 1996). In fact, condition [5], which characterizes invasion proofness, does

not ensure that the ESS will actually be attainable as the endpoint of a series of mutation/substitution events. There are examples of systems, in which arbitrarily small perturbations away from an ESS will cause the evolutionary dynamics to diverge from that ESS. Therefore, in addition to the invasion-proofness, we also need to distinguish attainable (or 'convergence stable' *sensu* Taylor, 1996a) singular points (evolutionary attractors) from dynamically unstable singular points. An evolutionarily singular strategy y^* is attainable if evolution proceeds towards higher $\hat{y}$ when $\hat{y} < y^*$, and towards lower $\hat{y}$ when $\hat{y} > y^*$. Since the direction of evolution is given by the sign of the selection gradient, equation [4], attainable evolutionarily singular points can be characterized by the condition

$$\left.\frac{d\lambda_y(\hat{y})}{d\hat{y}}\right|_{\hat{y}=y^*} < 0\,. \qquad [6]$$

Using conditions [5] and [6], the local evolutionary dynamics around any resident strategy $\hat{y}$ can be classified (Geritz *et al.*, 1998). An interesting phenomenon occurs when an evolutionarily singular strategy is attainable but not invasion-proof. That is to say, a series of mutation/substitution events converges to the evolutionarily singular strategy, but at that strategy, the population can be invaded by all mutants. In that case, the population is trapped at a fitness minimum, from which it can only escape when it undergoes evolutionary branching and becomes dimorphic, since any monomorphic population would be driven back to the evolutionarily singular point again (Metz *et al.*, 1996).

Conditions for ecological branching

After these general arguments, let us now proceed to derive the adaptive dynamics of ecotype and male mating type in our model. As is derived in detail in APPENDIX A, the growth rate of an ecological type mutant $(x,\hat{q})$, in a resident population $(\hat{x},\hat{q})$ is given by the expression (approximated for weak selection on females)

$$\lambda(x,\hat{x}) \approx -1+\frac{1}{4}\left(b-(b-2)\frac{g_c(x-\hat{x})g_K(\hat{x})}{g_K(x)}\right)\left(1+g_e(x-\hat{x})\right). \qquad [7]$$

This equation can best be understood by considering the two extreme regimes of small and very large birth rates. When b is small, the population can just sustain itself, and in that case the reduction of mate encounter rate caused by ecological differences governs the evolution of ecotype. Indeed, in that case equation [7] reduces to

$$\lambda(x,\hat{x}) \approx -\frac{1}{2}+\frac{1}{2}g_e(x-\hat{x}),\ \text{for } b \approx 2\,. \qquad [8]$$

As a consequence, $\lambda(x,\hat{x}) < \lambda(\hat{x},\hat{x})$. Selection will act against all mutant strategies, since all mutant males will suffer from reduced mate encounter rates.

In the regime of a very large birth rate the expression for the mutant growth rate reduces to

$$\lambda(x,\hat{x}) \propto 1-\frac{g_c(x-\hat{x})\,g_K(\hat{x})}{g_K(x)} \quad \text{for large } b\,. \qquad [9]$$

Note that the sign of the invasion fitness, and therefore the fate of the mutant, is completely determined by the competitive advantage of the mutant relative to the resident.

In the general case [7], the evolutionarily singular ecotypes can be found by computing the selection gradient

$$\left.\frac{\partial\lambda(x,\hat{x})}{\partial x}\right|_{x=\hat{x}} \approx -\frac{b-2}{2\sigma_K^2}\hat{x}\,. \qquad [10]$$

By checking the signs of the selection gradient for positive and negative $\hat{x}$, or according to condition [6], it can be seen that the ecological strategy $x^* = 0$ is an evolutionary attractor (i.e. an attainable evolutionarily singular point), provided that the population is viable ($b > 2$). Biologically, this means that a monomorphic population evolves towards the ecotype that matches the most abundant resources.

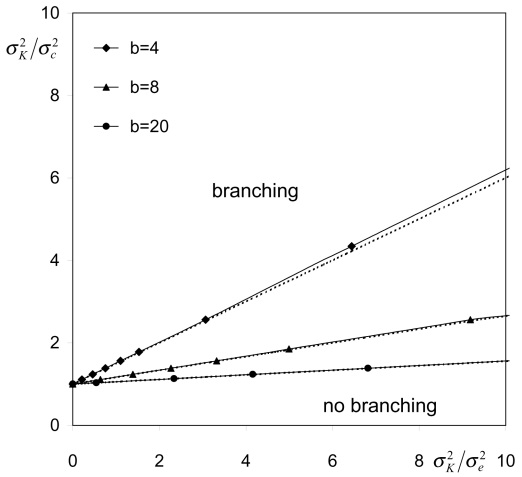


FIGURE 6 – CONDITIONS FOR BRANCHING OF ECOLOGICAL TYPE

The solid straight lines delimit the region of evolutionary branching of ecological type for different values of birth rate b. To the right on the σ_K^2/σ_e^2-axis, the effect of ecological differences on mate encounter rates becomes more important. Then, ecological branching occurs only when the width of the resource utilization function, σ_c, becomes increasingly smaller than the ecological resource variation σ_K. Branching occurs for a wider range of parameters when the birth rate is larger. The dashed lines correspond to the analytical predictions resulting from expression [12].

In order to determine the invasion-proofness of this strategy, we compute, again approximated for weak selection on female mating type, the second order derivative (all these results are derived in detail in APPENDIX A)

$$\left.\frac{\partial^2\lambda(x,\hat{x})}{\partial x^2}\right|_{x=\hat{x}=0} \approx \frac{1}{2}(b-2)\left(\frac{1}{\sigma_c^2}-\frac{1}{\sigma_K^2}\right)-\frac{1}{2}\frac{1}{\sigma_e^2}\,. \qquad [11]$$

From this equation, it follows that evolutionary branching of ecological type occurs when

$$\frac{\sigma_K^2}{\sigma_c^2} > 1+\frac{1}{b-2}\frac{\sigma_K^2}{\sigma_e^2}\,. \qquad [12]$$

In the limit where mating probabilities are independent of ecological differences (infinite σ_e), this expression reduces to the criterion $\sigma_c < \sigma_K$ (Doebeli & Dieckmann, 2000; see also FIGURE 1). In the general case, branching of ecological type occurs when the width of the resource utilization function is sufficiently smaller than the width of the resource distribution -'sufficiently' depending on the influence of ecological differences on mate encounter rates (FIGURE 6).

CONDITIONS FOR MATING TYPE BRANCHING

As is also derived in APPENDIX A, the invasion fitness, $\lambda(q,\hat{q})$ of a male mating type mutant $(\hat{x},q)$ in a resident population of type $(\hat{x},\hat{q})$ is given by the expression

$$\lambda(q,\hat{q}) = -\frac{1}{2} + \frac{1}{2}\frac{g_s(q)}{g_s(\hat{q})}\frac{Q(q,\hat{q})}{Q(\hat{q},\hat{q})}. \qquad [13]$$

Recall that the Gaussian function $g_s(q)$ represents viability selection on male mating type. The function $Q(q,\hat{q})$ denotes the expected number of q type offspring, produced by an arbitrary female, which is proportional to the probability that a female chooses a q- type male to mate with, and which depends on the distribution of female mating types in the population. Here this dependency is not made explicit: for details regarding this and all other results derived in this section, the reader is referred to APPENDICES A & B.

In particular, male mating type mutants can invade when

$$g_s(q)\,Q(q,\hat{q}) > g_s(\hat{q})\,Q(\hat{q},\hat{q}), \qquad [14]$$

which has a straightforward biological interpretation: evolution will maximize the product of male survival and reproductive success. This is also reflected by the selection gradient

$$\left.\frac{\partial\lambda(q,\hat{q})}{\partial q}\right|_{q=\hat{q}} = -\frac{1}{2}\hat{q}\frac{1}{\sigma_s^2} + \frac{1}{2}(\mu-\hat{q})\frac{1}{\sigma_m^2}, \qquad [15]$$

where the first term represents the stabilizing effect of viability selection on male trait, and the second term represent selection for an optimal match with female mating type (μ denotes the population average female mating type). Therefore, the evolution of male mating type will converge towards a compromise value between the optimum for viability selection ($\hat{q}=0$) and the optimum for mate competition ($\hat{q}=\mu$). This latter optimum is not constant in the course of evolution, however, since the distribution of female mating types is itself under weak directional selection towards optimal matching with male mating type. So eventually, both $\hat{q}$ and μ will converge to zero, the optimum for viability selection.

Again, the invasion proofness of this endpoint of monomorphic evolution can be checked by considering the second derivative of the invasion fitness

$$\left.\frac{\partial^2\lambda(q,\hat{q})}{\partial q^2}\right|_{q=\hat{q}=0} = \frac{1}{2}\left(-\frac{1}{\sigma_s^2} - \frac{1}{\sigma_m^2} + \frac{\sigma_p^2}{\sigma_m^4}\right), \qquad [16]$$

where σ_p^2 denotes the variance of female mating types present in the population. According to this expression, evolutionary branching of male mating type occurs when

$$\sigma_p^2 > \sigma_m^2 \left(1 + \frac{\sigma_m^2}{\sigma_s^2} \right). \qquad [17]$$

In the simplest case, when viability selection on male mating type is absent ($\sigma_s \to \infty$), evolutionary branching occurs only when the width of the female mating type distribution, σ_p, exceeds the width of the fertilization efficiency function, σ_m. One would expect this to occur when selection on female mating type is weak and when the mutation rate of the female mating type gene is higher. Indeed, numerical and analytical analysis (FIGURE 7, APPENDICES A & B), taking into account the full evolutionary dynamics of female mating type, have confirmed this expectation. Note that, in the general case, conditions for evolutionary branching become more restrictive for smaller σ_s^2, that is, for stronger viability selection on males.

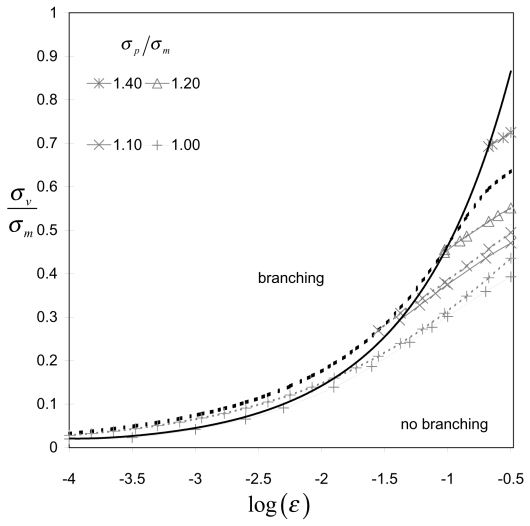


FIGURE 7 – CONDITIONS FOR BRANCHING OF MALE MATING TYPE

Along the horizontal axis, the cost of female mate choice varies (the parameter ε is a dimensionless quantity defined as η divided by the number of males, see APPENDIX A). The solid black line delimits the region of evolutionary branching of male mating type. As can be seen from the figure, branching occurs when selection on females is weak enough (as quantified by a small value of ε) and when the mutation rate of the female mating type gene is high enough relative to the mate choice specificity (upwards on the σ_v/σ_m -axis). The solid gray lines are lines of equal σ_p/σ_m. Note that the line $\sigma_p/\sigma_m = 1$, approaches the boundary of the branching region for small ε, that is to say, when selection on female mating type is weak, male mating type undergoes evolutionary branching as soon as the width of the female mating type distribution exceeds the width of the mating kernel. All solid lines result from numerical analysis of equations [A-7] and [B-1]. Also shown, as dashed lines, are the corresponding analytical approximations, resulting from equations [B-10] and [A-18]. This figure was computed for $\sigma_s/\sigma_m = 5.0$.

As mentioned before, there is an analogy between competition for ecological resources and competition for fertilizations. This analogy extends to the conditions for evolutionary branching: in the simplest case ($\sigma_s \to \infty, \sigma_e \to \infty$), conditions [12] and [17] reduce to $\sigma_c < \sigma_K$ and $\sigma_m < \sigma_p$, highlighting the analogy between resource utilization function and mate choice kernel (σ_c and σ_m) and between resource distribution and female mating type distribution (σ_K and σ_p). Note that, notwith-

standing the analogy, an important distinction between the two types of competition lies in the fact that the distribution of ecological resources is fixed, whereas the distribution of female mating types evolves in response to the male mating type(s) present in the population.

CONDITIONS FOR SYMPATRIC SPECIATION

It is important to realize that the occurrence of both ecological and mating type branching is necessary but not sufficient for sympatric speciation. Besides polymorphism of mating types and ecotypes, it is also required that, during speciation, linkage disequilibrium develops between ecological and mating strategies (Felsenstein, 1981). Only then will evolutionary branching of ecotype and mating type result in the evolution of reproductively isolated and –at the same time– ecologically differentiated species.

We investigated the development of linkage disequilibrium after evolutionary branching by a technique similar to the one used above. Under the assumption that the resident population is dimorphic for both male mating type and ecotype, one again writes down the invasion fitness of a mutant and solves for the attractors of the dimorphic evolutionary dynamics. Together with equations for the evolution of female mating types, this is a complete description of the adaptive dynamics, from which the expected correlation between ecotype and male mating type (which is a measure for the linkage disequilibrium) can be derived (APPENDIX C). The results of this analysis show that there is a region in parameter space where male mating type and ecotype become correlated with another (FIGURE 8). On the other hand, FIGURE 8 also illustrates that evolutionary branching indeed not inevitably results in sympatric speciation since, in the complementary region of parameter space, linkage disequilibrium does not build up.

Two processes will determine whether linkage disequilibrium can develop. On the one hand, competition within ecotype (i.e. between individuals of identical ecotype) will tend to eliminate polymorphism of male mating type within ecotype and enlarge the correlation between ecotypes and mating types. On the other hand, mating between ecotypes will tend to destroy any linkage disequilibrium. Because of this, one would intuitively expect that linkage disequilibrium would develop more easily when the encounter rate between individuals of different ecological types is reduced (smaller σ_e). Then, mating between different ecotypes will occur only rarely, even if individuals are of matching mating type. Indeed, Figure 8 shows that correlations develop only for sufficiently small σ_e. Here, 'sufficiently small' relates to the ecological separation between ecotypes after ecological branching, Δx: in the region where linkage disequilibrium develops, we have $\sigma_e < \Delta x$, and at its border $\sigma_e = \Delta x$.

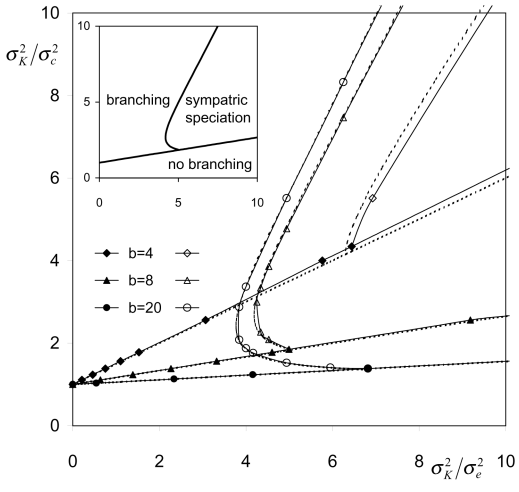


FIGURE 8 – CONDITIONS FOR SYMPATRIC SPECIATION

When ecotype and male mating type are both dimorphic, correlations may develop between ecotype and mating types, resulting in the evolution of reproductively isolated and ecologically differentiated species. In an infinite population, such a correlation develops only in a limited region of parameter space (inset). This region is delimited by a straight line bordering the region of evolutionary branching (filled symbols) and another line (open symbols), which can be computed by considering the adaptive dynamics of a population dimorphic for both ecotype and male mating type (see the main text and APPENDIX C for details). In the remaining part of the parameter space where ecological branching is possible, correlations can only evolve in finite populations. All solid lines result from numerical analysis. The dashed lines represent the corresponding analytical predictions (resulting from equations [12] and [C-5] where $x^* = \sigma_e$).

Simulations indicate that the region of parameter space where a linkage disequilibrium does build up corresponds to those conditions under which male mating type branching results in a bimodal female mating type distribution (as suggested in FIGURE 2D) and, correspondingly, in a high degree of assortative mating. For parameters outside this region, male mating type branching usually results in a broad unimodal distribution of female mating types. The evolution of a bimodal female mating type distribution, corresponding to branching in female mating types, requires diversifying frequency dependent selection on female mating type. In our case, this is caused by the association between mating types and ecological type, giving extreme mating types an advantage due to competition avoidance. We conjecture that other forms of frequency-dependent selection will have similar effects, but this requires further investigation.

GENERALIZATION OF THE MATHEMATICAL RESULTS

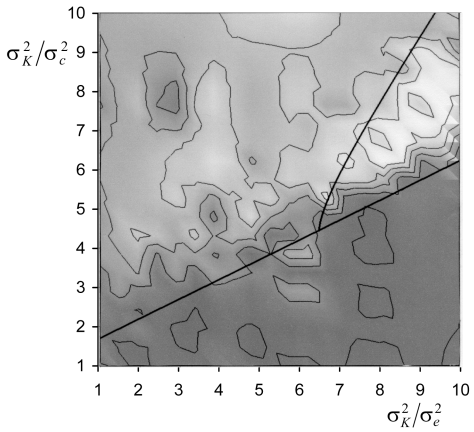
DIPLOID/MULTILOCUS GENETICS AND SMALL POPULATION SIZE

The results presented in the previous section are strictly valid only for single locus haploid genetic systems and for sufficiently large populations (such that stochasticity can be ignored). In order to check whether the analytical results hold in a more general context of multilocus genetics we ran simulations with different genetic systems underlying the traits, each for a large number of parameter combinations, and we measured the correlation between ecological and mating types as an indicator of the occurrence of speciation. FIGURE 9 shows the result of one such experiment, where we assumed single locus diploid genetics underlying all traits.

The conditions for branching of mating types are predicted well by the theory (data not shown). For ecological branching and subsequent speciation we find that there are two important qualitative differences between theoretical predictions and simulation results.

FIGURE 9 – A COMPARISON OF THE ANALYTICAL PREDICTIONS WITH INDIVIDUAL-BASED SIMULATIONS

A large number of simulations were run for different combinations of the parameters σ_c, σ_e and σ_K, thus varying the ecological selection regime. For these parameter combinations (other parameters as in FIGURE 3), the figure shows the association between ecological type and mating type. This is measured as the correlation between these traits (averaged over 1000 generations) and indicated on a gray scale with contour lines at the values 0, 0.2, 0.4, 0.6 and 0.8 (white indicates high, black indicates low correlation). Also shown in thick black lines are the analytical predictions for the boundaries of the branching region and the region where a correlation between ecological type and mating type exists (also shown in FIGURE 8). These analytical predictions are based on a large population approximation where stochasticity is ignored. The region where a strong



association between mating types and ecotype evolves -this is the light gray / white area- falls within the analytically predicted region, but does not completely fill it, particularly not for small σ_K^2/σ_e^2. Another striking feature is that speciation occurs for a considerably larger range of parameters than would be predicted from the deterministic approximation of the population dynamics. As in the FIGURES 3–5, population sizes in the simulations were about 1000 individuals per species.

First, conditions for branching are more restrictive than predicted when mate encounter rates are not affected by ecological differences (for large σ_e). This observation is in accordance with the results of Dieckmann & Doebeli (1999), who noted that the conditions for branching agree well with predictions based on an asexual model when mating probabilities depend on ecological type, but are more restrictive when mating probabilities are independent of ecological traits, instead depending on a neutral marker trait (in our model male and female mating type).

Second, the parameter region in which mating types and ecological type become correlated with another –this is the region where sympatric speciation occurs– is much larger than predicted. This discrepancy can partly be explained by the fact that the population sizes in our simulations are not so large that stochasticity can be ignored, as we assumed in the mathematical analysis. In the simulations, random fluctuations of the linkage disequilibrium between ecological and mating type loci occur, caused by the stochasticity of demographic processes in finite populations. Due to the evolutionary dynamics, such small fluctuations may be

enlarged, if they exceed a certain threshold, resulting in a larger linkage disequilibrium and eventually speciation. This effect was also described by Dieckmann & Doebeli (1999). Another factor that may explain why speciation seems to occur for a wider range of parameters than expected, is that there is some amount of genetic variation of male mating type in the individual based simulations (which was neglected in the adaptive dynamics approximation). This genetic variation enlarges the 'assortativeness' of mating, which may facilitate speciation.

For larger populations and multi-locus genetics, results are similar, except that the waiting time until speciation increases. For a very large number of loci, results were also checked using a quantitative genetics approximation. Again, sympatric speciation occurred for a wide range of parameters (similar to FIGURE 9).

DISCUSSION

Our model represents a first step towards understanding the multitude of entangled processes that underlie sympatric speciation. We have focused on the interplay between ecological interactions as a source of biological diversity and sexual selection as the mechanism underlying reproductive isolation. The results of our analysis show that ecological differentiation and the evolution of assortative mating are mutually dependent processes that are both required for sympatric speciation. Ecological differentiation arises naturally from evolutionary branching of competitive strategies (as determined by ecotype). Assortative mating results from evolutionary branching of mating strategies (male mating type) automatically followed by the genetic association of matching male and female mating types. Sympatric speciation is completed when, in addition, a linkage disequilibrium develops between ecotypes and mating types, giving rise to reproductively isolated and, at the same time, ecologically differentiated daughter species.

On an abstract level, ecological and mating type branching can both be understood as the outcome of a competition process in which the optimal competitive strategy is determined by the distribution of resources (ecological resources or mating opportunities, respectively) and by the competitive behavior of other individuals. At first sight, it might seem an optimal competitive strategy to specialize on the most abundant resource. However, it might also pay to specialize on less abundant resources, thus avoiding competition with other individuals. The latter applies particularly when the variation of resources is large. These considerations translate into a feedback between ecological and evolutionary processes, which drive a monomorphic population towards the optimum of the resource distribution, but may there induce disruptive selection resulting in evolutionary branching. For ecological resource competition and mate competition alike, this occurs only when the variation 'resources' (ecological resources or female mating types, respectively) is large enough. For ecological competition, this implies that individuals should be ecological specialists rather than generalists. For mate competi-

tion, it implies that mate choice should be sufficiently specific or that selection on female mate choice should be weak.

In very large populations, the required linkage disequilibrium between ecotype and mating types will only develop when individuals that differ ecologically also have a lower probability of mating with each other. This mate choice with respect to ecotype has to be specific enough in order to establish a linkage disequilibrium, but not too specific, since, in that case, evolutionary branching of ecotype would be prohibited. In small populations, however, the conditions for sympatric speciation are far less stringent, as a result of stochasticity. Small random fluctuations of genetic correlations between ecotype and mating types can be enlarged by the ecological dynamics to a strong linkage disequilibrium. This important effect of stochasticity was also noted by Dieckmann & Doebeli (1999), and it illustrates the usefulness of a combined computer-simulation and analytical approach.

Although we have chosen for a rather general modeling approach, we would like to stress that we have imposed a number of restrictions, the alleviation of which provides ample opportunities for future research. For example, in our analysis we have treated ecological branching and mating type branching as largely separate processes, assuming that the coupling between ecotype dynamics and mating type dynamics becomes important only later, when the linkage disequilibrium between ecotype and mating types establishes itself. This approach has been motivated and checked by numerical studies, but from a methodological point of view, it is important to note that this leaves out of consideration modes of evolutionary branching that result from the coupling of ecotype and mating type dynamics. The theory of such higher dimensional branching is rather complicated and is subject of current theoretical research.

A number of key parameters of our model were assumed to be constant and not subject to evolution. This may not be adequate, particularly not for the parameters σ_c and σ_m, since resource utilization characteristics (σ_c) and the specificity of mate choice (σ_m) are themselves likely to be subject to evolutionary change. It would therefore be interesting to consider as a second step models that include more of the mechanisms and trade-offs associated with resource utilization and mate choice characteristics.

Other elaborations may include the modeling of different ecological interactions or other mechanisms of mate choice. Moreover, a spatial version of the model may be used to gain insight in the influence of spatial pattern formation on sympatric speciation. In order to study sympatric speciation in its purest form, models usually consider only well-mixed populations. This excludes the possibility of spatial pattern formation, which is all but absent from most biological systems. In addition, from a theoretical viewpoint, it is well conceivable that adding a small spatial component may greatly enlarge the potential for sympatric speciation. This is, for instance, because the stochasticity of local interactions with a limited number of neighbors may greatly facilitate the development of linkage disequilibrium re-

quired for speciation or because spatial heterogeneity may enhance evolutionary branching.

APPENDIX A — CONDITIONS FOR EVOLUTIONARY BRANCHING

To find the invasion fitness of a mutant (x,q) in a resident population $(\hat{x},\hat{q})$, we write a differential equation describing the dynamics of the number of mutants when rare

$$\frac{dn}{dt} = \underbrace{-n}_{\text{death}} + \underbrace{\tfrac{1}{2} n\, S(q)\big(1-M(x,\hat{x})\big)Q_M(x,q,\hat{x},\hat{q})}_{\text{production and survival of male mutants}} + \underbrace{\tfrac{1}{2} n\big(1-M(x,\hat{x})\big)Q_F(x,q,\hat{x},\hat{q})}_{\text{production and survival of female mutants}} + O(n^2), \quad \text{[A-1]}$$

where n denotes the density of the mutant before selection, and Q_M (Q_F) denotes the number of mutant offspring produced per mutant male (female). Analogously to the stochastic simulation model, $S(q) = g_s(q)$ represents direct viability selection on male mating type and $M(x,\hat{x})$ defines density dependent mortality due to ecological resource competition:

$$M(x,\hat{x}) = \gamma \frac{(N_M + N_F)\, g_c(x-\hat{x})}{g_K(x)}, \quad \text{[A-2]}$$

where N_M and N_F are the densities of resident males and females.

Formally, we should have written more complicated equations for the mutant dynamics, at least, when we want to consider mutants that differ from the resident in both mating type and ecological type. Such double mutants can however be neglected, since we will consider only single mutants (x,q) where either $x = \hat{x}$ or $q = \hat{q}$.

Now, let us define the mutant per capita birth rates Q_M and Q_F. The probability that a mutant male of type (x,q) mates with a female of type $(\hat{x},\hat{q})$ and female mating type p is given by the expression

$$\frac{g_m(p-q)\, g_e(x-\hat{x})}{\eta + N_M\, g_m(p-\hat{q})} = g_e(x-\hat{x}) \frac{1}{N_M} \frac{g_m(p-q)}{\varepsilon + g_m(p-\hat{q})}, \quad \text{[A-3]}$$

where $\varepsilon = \eta / N_M$. Formally, N_M depends on $\hat{x}$ and $\hat{q}$, but since ε will generally be small we will ignore these higher order dependencies and treat ε as a parameter from here on.

To find Q_M, the mating probability [A-3] has to be multiplied by the density of mating type p females, and integrated over all possible female mating types. If we denote the frequency distribution of female mating types in the population as $f(p)$, then

$$Q_M(x,q,\hat{x},\hat{q}) = g_e(x-\hat{x}) \frac{N_F}{N_M} Q(q,\hat{q}), \quad \text{[A-4]}$$

where

$$Q(q,\hat{q}) = \frac{b}{2}\int_{-\infty}^{\infty} f(p)\frac{g_m(p-q)}{\varepsilon + g_m(p-\hat{q})}dp\,. \qquad \text{[A-5]}$$

The function $Q(q,\hat{q})$ can be interpreted as the expected number of q-offspring that will be produced by an average resident female. In particular, we will use that, if selection on females is weak, $Q(\hat{q},\hat{q}) \approx b/2$. This corresponds to saying that females will produce close to b offspring when they mate with a resident male.

Similarly, to find Q_F, the probability that a mutant female mates, is integrated over all possible female mating types, weighted with respect to their frequency, which yields

$$Q_F(x,q,\hat{x},\hat{q}) = \frac{b}{2}\int_{-\infty}^{\infty} f(p)\frac{N_M\, g_m(p-\hat{q})\, g_e(x-\hat{x})}{\eta + N_M\, g_m(p-\hat{q})\, g_e(x-\hat{x})}\,dp = Q(\hat{q},\hat{q}) + O(\varepsilon)\,. \qquad \text{[A-6]}$$

Equation [A-1] can now be rewritten using equations [A-4] and [A-6] together with $N_M / N_F = g_s(\hat{q})$, to give $\lambda(x,q,\hat{x},\hat{q})$, the per capita growth rate of the mutant in the resident population $(\hat{x},\hat{q})$:

$$\lambda(x,q,\hat{x},\hat{q}) = \frac{1}{n}\frac{dn}{dt} = -1 + \frac{1}{2}\big(1 - M(x,\hat{x})\big)\left(g_e(x-\hat{x})\frac{g_s(q)}{g_s(\hat{q})}Q(q,\hat{q}) + Q(\hat{q},\hat{q}) + O(\varepsilon)\right). \text{[A-7]}$$

We assume that the resident population is in population dynamical equilibrium, which implies that a 'mutant' $(x=\hat{x}, q=\hat{q})$ should have a per capita growth rate equal to zero. According to equations [A-2] and [A-7], this condition implies that

$$N = \frac{g_K(\hat{x})}{\gamma}\left(1 - \frac{1}{Q(\hat{q},\hat{q})}\right). \qquad \text{[A-8]}$$

To find the invasion fitness of an ecological type mutant, we substitute $q=\hat{q}$ into equation [A-7], which yields

$$\lambda(x,\hat{q},\hat{x},\hat{q}) = -1 + \frac{1}{2}\left(Q(\hat{q},\hat{q}) - \big(Q(\hat{q},\hat{q})-1\big)\frac{g_c(x-\hat{x})\, g_K(\hat{x})}{g_K(x)}\right)\big(g_e(x-\hat{x}) + 1 + O(\varepsilon)\big)\,. \text{[A-9]}$$

For small ε, this equation becomes independent of $\hat{q}$, and approaches equation [7], which is interpreted biologically in the main text.

For a male mating type mutant, the invasion fitness reduces to

$$\lambda(\hat{x},q,\hat{x},\hat{q}) = -\frac{1}{2} + \frac{1}{2}\frac{g_s(q)}{g_s(\hat{q})}\frac{Q(q,\hat{q})}{Q(\hat{q},\hat{q})}\,, \qquad \text{[A-10]}$$

which is independent of $\hat{x}$ and identical to equation [13] .

Up to now, we have ignored the dynamics of the frequency distribution of female mating types $f(p)$. As it turns out, we do not need to know the full distribution $f(p)$. Instead, we can suffice with the functions m_0, m_1 and m_2, where

$$m_k(\hat{q}) = \int_{-\infty}^{\infty}(p-\hat{q})^k\, f(p)\frac{g_m(p-\hat{q})}{\varepsilon + g_m(p-\hat{q})}dp\,. \qquad \text{[A-11]}$$

As will be shown in detail in APPENDIX B, where the dynamics of $f(p)$ is treated, we have

$$\text{for all } \hat{q}: \quad \frac{m_1(\hat{q})}{m_0(\hat{q})} = \mu - \hat{q} \quad \text{and} \quad \frac{m_2(\hat{q})}{m_0(\hat{q})} \approx \sigma_p^2 . \qquad \text{[A-12]}$$

These expressions can be interpreted as the first and second moment of the distribution of mating opportunities, which turn out to be related to the mean (μ) and variance (σ_p^2) of the female mating type distribution (APPENDIX B).

To find the evolutionary attractors $(\bar{x},\bar{q})$ of the monomorphic dynamics, we need to compute the selection gradients

$$\lambda_x(\hat{x},q^*) = \left.\frac{\partial\lambda(x,q,\hat{x},\hat{q})}{\partial x}\right|_{\substack{x=\hat{x}\\ q=\hat{q}=q^*}} = -\hat{x}\,\frac{Q(q^*,q^*)-1}{\sigma_K^2}, \qquad \text{[A-13]}$$

and

$$\lambda_q(\hat{q},x^*) = \left.\frac{\partial\lambda(x,q,\hat{x},\hat{q})}{\partial q}\right|_{\substack{x=\hat{x}=x^*\\ q=\hat{q}}} = -\frac{1}{2}\hat{q}\frac{1}{\sigma_s^2} + \frac{1}{2}(\mu-\hat{q})\frac{1}{\sigma_m^2}, \qquad \text{[A-14]}$$

where we have used the expression [A-12] for the first moment of the distribution of mating opportunities.

When $\lambda_x(\hat{x},q^*)>0$, selection acts to increase $\hat{x}$. Alternatively, when $\lambda_x(\hat{x},q^*)<0$, selection acts to decrease $\hat{x}$. With similar conditions for $\hat{q}$, where we additionally postulate that $\mu\to 0$ in the course of evolution (see APPENDIX B), it follows that (x^*,q^*) must satisfy $\lambda_x(x^*,q^*)=0$ and $\lambda_q(q^*,x^*)=0$, implying that $(x^*,q^*)=(0,0)$. This evolutionarily singular point is an evolutionary attractor when

$$\left.\frac{\partial\lambda_x(\hat{x},0)}{\partial\hat{x}}\right|_{\hat{x}=0} = -\frac{Q(0,0)-1}{\sigma_K^2} < 0 \quad \text{and} \quad \left.\frac{\partial\lambda_q(\hat{q},0)}{\partial\hat{q}}\right|_{\hat{q}=0} = -\frac{1}{2}\frac{1}{\sigma_s^2} < 0 \quad \Leftrightarrow$$

$$b > \frac{2}{\int_{-\infty}^{\infty} f(p)\frac{g_m(p)}{\varepsilon+g_m(p)}dp} \approx 2, \qquad \text{[A-15]}$$

the latter condition implying that there should be a viable population.

Evolutionary branching occurs only when the population at $(x^*,q^*)=(0,0)$ is located at a fitness minimum with respect to the mutant strategy, in other words, when

$$\lambda_{xx}(x^*,q^*) = \left.\frac{\partial^2\lambda(x,q,\hat{x},\hat{q})}{\partial x^2}\right|_{\substack{x=\hat{x}=x^*\\ q=\hat{q}=q^*}} > 0, \qquad \text{[A-16]}$$

and

$$\lambda_{qq}(q^*,x^*) = \left.\frac{\partial^2\lambda(x,q,\hat{x},\hat{q})}{\partial q^2}\right|_{\substack{x=\hat{x}=x^*\\ q=\hat{q}=q^*}} > 0. \qquad \text{[A-17]}$$

Substituting the evolutionary attractor $(x^*, q^*) = (0,0)$ into equation [A-17] yields the following condition for branching of male mating type

$$\lambda_{qq}(0,0) = \frac{1}{2}\left(-\frac{1}{\sigma_s^2} - \frac{1}{\sigma_m^2} + \frac{1}{\sigma_m^4}\frac{M_2(0)}{M_0(0)} \right) > 0 . \qquad \text{[A-18]}$$

Equations [A-12] and [A-18], approximated for small mutation rates, combine into the condition [17]

$$\sigma_p^2 > \sigma_m^2 \left(1 + \frac{\sigma_m^2}{\sigma_s^2} \right). \qquad \text{[A-19]}$$

Consequently, male mating strategy undergoes evolutionary branching when the variation of female mating strategies exceeds a threshold of the order of σ_m, the scale that determines the specificity of mate choice.

Furthermore, branching of ecological type x occurs when

$$\lambda_{xx}(0,0) = \left(Q^* - 1\right)\left(\frac{1}{\sigma_c^2} - \frac{1}{\sigma_K^2} \right) - \frac{1}{2}\frac{1}{\sigma_e^2}\left(1 + O(\varepsilon)\right) > 0 , \qquad \text{[A-20]}$$

with $Q^* = Q(0,0)$.

In the limit of infinite σ_e, the condition for branching reduces to the well-known form $\sigma_c < \sigma_K$. In the general case, we find condition [12]

$$\frac{\sigma_K^2}{\sigma_c^2} > 1 + \frac{1}{2\left(Q^* - 1\right)}\frac{\sigma_K^2}{\sigma_e^2} + O(\varepsilon) \approx 1 + \frac{1}{b-2}\frac{\sigma_K^2}{\sigma_e^2} . \qquad \text{[A-21]}$$

APPENDIX B — DYNAMICS OF FEMALE MATING TYPE

If the female mating type p is determined by a single locus haploid genotype, then $f(p)$ must satisfy

$$f(p) = \underbrace{\frac{1}{2}\bar{g}_v * f(p)}_{\substack{\text{contribution via} \\ \text{male parent}}} + \underbrace{\frac{1}{2Q(\hat{q},\hat{q})}\bar{g}_v * \left(\frac{b}{2} f(p) \frac{g_m(p-\hat{q})}{\varepsilon + g_m(p-\hat{q})} \right)}_{\text{contribution via female parent}}, \qquad \text{[B-1]}$$

where $\bar{g}_v$ denotes the mutation kernel

$$\bar{g}_v(p) = \frac{1}{\sigma_v\sqrt{2\pi}} \exp\left(-\frac{1}{2}\frac{p^2}{\sigma_v^2} \right), \qquad \text{[B-2]}$$

and $*$ denotes the convolution operator

$$u * v(p) = \int_{-\infty}^{\infty} u(z)\, v(z-p)\, dz . \qquad \text{[B-3]}$$

Let us now write $f(p)$ as a series expansion.

$$f(p) = g_p(p-\mu)\left(1 + \sum_{n=3}^{\infty} \alpha_n H_n\left(\frac{p-\mu}{\sigma_p} \right) \right). \qquad \text{[B-4]}$$

The functions $H_n(p)$ are so called Hermite polynomials, defined as

$$H_n(p) = (-1)^n e^{\frac{1}{2}p^2} \frac{d^n}{dp^n} e^{-\frac{1}{2}p^2} . \qquad \text{[B-5]}$$

In particular, $H_0(p) = 1$, $H_1(p) = p$ and $H_2(p) = p^2 - 1$. It can be shown that the series at the right hand side of equation [B-4] converges uniformly towards $f(p)$.

Multiplying both sides of equation [B-1] with $H_1\left((p-\mu)/\sigma_p\right)$ and integrating over all p yields

$$\mu = \frac{\int_{-\infty}^{\infty} p\, f(p) \frac{g_m(p-\hat{q})}{\varepsilon + g_m(p-\hat{q})} dp}{\int_{-\infty}^{\infty} f(p) \frac{g_m(p-\hat{q})}{\varepsilon + g_m(p-\hat{q})} dp} , \qquad \text{[B-6]}$$

which is an expression that relates the first moment of the distribution of mating opportunities to the average female mating type (equation [A-12]). Stationary solutions $f(p)$ are obtained only when $\mu = \hat{q}$. Here we omit the mathematical proof, but this result can explained biologically by the fact that only one directed selection pressure acts on the female mating type distribution, and this will lead towards exact matching of the mean of the female mating type distribution with the resident male mating type. In deriving equation [B-6], we have used equation [B-4] as an approximation for $f(p)$ together with the orthogonality property of Hermite polynomials

$$\int_{-\infty}^{\infty} H_n(p)\, H_m(p)\, e^{-\frac{1}{2}p^2} dp = 0 \quad \text{if} \quad n \neq m . \qquad \text{[B-7]}$$

Similarly, multiplying both sides of equation [B-1] with $H_2\left((p-\mu)/\sigma_p\right)$ and integrating over all p gives an expression for σ_p^2

$$\sigma_p^2 = 2\sigma_v^2 + \frac{\int_{-\infty}^{\infty} (p-\hat{q})^2\, f(p) \frac{g_m(p-\hat{q})}{\varepsilon + g_m(p-\hat{q})} dp}{\int_{-\infty}^{\infty} f(p) \frac{g_m(p-\hat{q})}{\varepsilon + g_m(p-\hat{q})} dp} . \qquad \text{[B-8]}$$

Now it also follows immediately that $m_2(q)/m_0(q) = \sigma_p^2 - 2\sigma_v^2 \approx \sigma_p^2$ (equation [A-12]).

In order to express σ_p in the parameters of the model, we can make the following approximation

$$\frac{g_m(p)}{\varepsilon + g_m(p)} \approx \beta \int_{-\vartheta}^{\vartheta} \exp\left(-\frac{1}{2}\left(\frac{z-p}{\frac{1}{2}\sigma_m} \right)^2 \right) dz , \qquad \text{[B-9]}$$

where $\vartheta = \sigma_m \sqrt{-2\ln(\varepsilon)}$ and where β is an unimportant proportionality constant. Under this approximation and neglecting the higher order Hermite polynomial terms in equation [B-4], it can be derived that σ_p satisfies

$$\tilde{\sigma}_v^2 = \frac{\tilde{\sigma}_p^4\,\tilde{\vartheta}}{\sqrt{2\pi}\left(\tilde{\sigma}_p^2+\tfrac{1}{4}\right)^{3/2}} \frac{e^{-\frac{1}{2}\frac{\tilde{\vartheta}^2}{\tilde{\sigma}_p^2+\frac{1}{4}}}}{\operatorname{erf}\left(\frac{1}{2}\sqrt{2}\frac{\tilde{\vartheta}}{\sqrt{\tilde{\sigma}_p^2+\frac{1}{4}}}\right)}, \qquad \text{[B-10]}$$

with $\tilde{\vartheta} = \sqrt{-2\ln(\varepsilon)}$, $\tilde{\sigma}_p = \sigma_p/\sigma_m$ and $\tilde{\sigma}_v = \sigma_v/\sigma_m$. FIGURE 7 shows the parameter region in which branching occurs, following from equation [B-10] as well as numerically calculated from equations [A-7] and [B-1].

APPENDIX C — DIMORPHIC DYNAMICS

Suppose that the resident population is dimorphic for ecological type and male mating type with character values x_1, x_2, q_1 and q_2. Moreover, consider the female mating type distributions $f_{i,j}(p)$ for genotype (x_i, q_j). Because of the symmetry of the model, we will consider only symmetric cases here, and therefore denote

$$\begin{aligned} \hat{q} &= \hat{q}_1 = -\hat{q}_2\,, \\ \hat{x} &= \hat{x}_1 = -\hat{x}_2\,, \\ f_+(p) &= 2f_{1,1}(p) = 2f_{2,2}(-p)\,, \\ f_-(p) &= 2f_{1,2}(p) = 2f_{2,1}(-p)\,, \\ \text{with } &\int_{-\infty}^{\infty} f_+(p) + f_-(p)\,dp = 1\,. \end{aligned} \qquad \text{[C-1]}$$

As a measure of correlation between ecological and male mating type, we define

$$\rho = \int_{-\infty}^{\infty} f_+(p)\,dp\,. \qquad \text{[C-2]}$$

A derivation similar to the one presented in APPENDIX A, enables us to find the invasion fitness of a rare mutant (x,q) in a resident population consisting of the types $(\hat{x},\hat{q})$, $(\hat{x},-\hat{q})$, $(-\hat{x},\hat{q})$ and $(-\hat{x},-\hat{q})$. Analogously to equation [A-7], we find

$$\begin{aligned} \lambda(x,q,\hat{x},\hat{q}) = -1 + \frac{1}{2}\Bigg(& 1 - \frac{\big(g_c(x-\hat{x}) + g_c(x+\hat{x})\big)g_K(\hat{x})}{\big(1+g_c(2\hat{x})\big)g_K(x)}\left(1 - \frac{1}{Q_2(\hat{q},\hat{x})}\right)\Bigg)\cdot \\ & \left(\frac{g_s(q)}{g_s(\hat{q})}\int_{-\infty}^{\infty}\big(f_+(p)+f_-(p)\big)\cdot\right. \\ & \frac{g_m(p-q)\big(\rho\, g_e(x-\hat{x}) + (1-\rho)\,g_e(x+\hat{x})\big) + g_m(p+q)\big(\rho\, g_e(x+\hat{x}) + (1-\rho)\,g_e(x-\hat{x})\big)}{2\varepsilon + g_m(p-\hat{q})\big(\rho + (1-\rho)\,g_e(2\hat{x})\big) + g_m(p+\hat{q})\big(\rho\, g_e(2\hat{x}) + (1-\rho)\big)}\,dp \\ & + \int_{-\infty}^{\infty}\big(f_+(p)+f_-(p)\big)\cdot \\ & \left.\frac{g_m(p-\hat{q})\big(\rho\, g_e(x-\hat{x}) + (1-\rho)\,g_e(x+\hat{x})\big) + g_m(p+\hat{q})\big(\rho\, g_e(x+\hat{x}) + (1-\rho)\,g_e(x-\hat{x})\big)}{2\varepsilon + g_m(p-\hat{q})\big(\rho\, g_e(x-\hat{x}) + (1-\rho)\,g_e(x+\hat{x})\big) + g_m(p+\hat{q})\big(\rho\, g_e(x+\hat{x}) + (1-\rho)\,g_e(x-\hat{x})\big)}\,dp\right), \end{aligned} \qquad \text{[C-3]}$$

with

$$Q_2(\hat{q},\hat{x}) = \frac{b}{2}\int_{-\infty}^{\infty}\left(f_+(p)+f_-(p)\right)\cdot \frac{g_m(p-\hat{q})\left(\rho+(1-\rho)g_e(2\hat{x})\right)+g_m(p+\hat{q})\left(\rho\, g_e(2\hat{x})+(1-\rho)\right)}{2\varepsilon+g_m(p-\hat{q})\left(\rho+(1-\rho)g_e(2\hat{x})\right)+g_m(p+\hat{q})\left(\rho\, g_e(2\hat{x})+(1-\rho)\right)}dp\,. \qquad \text{[C-4]}$$

Attractors $\left(x^*,q^*\right)$ of the dimorphic dynamics satisfy

$$\left.\frac{\partial\lambda(x,q,\hat{x},\hat{q})}{\partial q}\right|_{\substack{x=\hat{x}=x^*\\ q=\hat{q}=q^*}} = -\frac{1}{2}\left(\frac{q^*}{\sigma_s^2}+\frac{q^*}{\sigma_m^2}-\frac{1}{\sigma_m^2}\frac{L_1(x^*,q^*)}{L_0(x^*,q^*)}\right)=0 \quad \text{and}$$

$$\left.\frac{\partial\lambda(x,q,\hat{x},\hat{q})}{\partial x}\right|_{\substack{x=\hat{x}=x^*\\ q=\hat{q}=q^*}} = x^*\left(\frac{1}{\sigma_c^2}\frac{2g_c(2x^*)}{1+g_c(2x^*)}-\frac{1}{\sigma_K^2}\right)\left(Q_2(q^*,x^*)-1\right) \qquad \text{[C-5]}$$

$$-x^*\frac{1}{2}\frac{1}{\sigma_e^2}\frac{2g_e(2x^*)}{1+g_e(2x^*)}\left(\frac{\tilde{L}_0(x^*,q^*)}{L_0(x^*,q^*)}+O(\varepsilon)\right)=0\,,$$

with

$$L_k(x^*,q^*) = \int_{-\infty}^{\infty}(p-q^*)^k\left(f_+(p)+f_-(p)\right)\cdot \frac{g_m(p-q^*)\left(\rho+(1-\rho)g_e(2x^*)\right)+g_m(p+q^*)\left(\rho\, g_e(2x^*)+(1-\rho)\right)}{2\varepsilon+g_m(p-q^*)\left(\rho+(1-\rho)g_e(2x^*)\right)+g_m(p+q^*)\left(\rho\, g_e(2x^*)+(1-\rho)\right)},$$

$$\tilde{L}_0(x^*,q^*) = \int_{-\infty}^{\infty}\left(f_+(p)+f_-(p)\right)\cdot \frac{(1-\rho)g_m(p-q^*)\left(1+g_e(2x^*)\right)+\rho\, g_m(p+q^*)\left(1+g_e(2x^*)\right)}{2\varepsilon+g_m(p-q^*)\left(\rho+(1-\rho)g_e(2x^*)\right)+g_m(p+q^*)\left(\rho\, g_e(2x^*)+(1-\rho)\right)}. \qquad \text{[C-6]}$$

Note that for $\rho=1/2$, $\tilde{L}_0(x^*,q^*)=L_0(x^*,q^*)$.

We can describe the dynamics of $f_+(p)$ and $f_-(p)$ by deriving equations for the genotypes $\left(x_i,q_j\right)$ similar to equation [B-1]

$$f_{i,j}(p) = \frac{1}{8\,Q_2(q^*,x^*)}\sum_{\substack{k\in\{1,2\}\\ l\in\{1,2\}}}\bar{g}_v * \int_{-\infty}^{\infty}T_{k,l}^{i,j}(p,z)+T_{k,l}^{i,j}(z,p)+T_{i,l}^{k,j}(p,z)+ T_{i,l}^{k,j}(z,p)+T_{k,j}^{i,l}(p,z)+T_{k,j}^{i,l}(z,p)+T_{i,j}^{k,l}(p,z)+T_{i,j}^{k,l}(z,p)\,dz\,, \qquad \text{[C-7]}$$

where the terms $T_{i,j}^{k,l}(p_1,p_2)$ denote the contributions by a mating of a $\left(p_1,x_i,q_j\right)$ female with a $\left(p_2,x_k,q_l\right)$ male:

$$T_{k,l}^{i,j}(p_1,p_2) = f_{i,j}(p_1)f_{k,l}(p_2)g_m(p_1-q_l)g_e(x_i-x_k)\Big/\Big(2\varepsilon+g_m(p_1-\hat{q})\big(\rho\, g_e(x_i-\hat{x}) +(1-\rho)g_e(x_i+\hat{x})\big)+g_m(p_1+\hat{q})\big(\rho\, g_e(x_i+\hat{x})+(1-\rho)g_e(x_i-\hat{x})\big)\Big). \qquad \text{[C-8]}$$

In order to investigate the conditions under which a correlation between ecological types and mating types develops, equations [C-5] and [C-7] can be solved numeri-

cally, yielding the equilibrium distributions of female mating types, from which ρ can be calculated (equation [C-2]).